

## **BUCKMAN'S PARADOX: CONSTRAINTS ON AMMONOID ORNAMENT AND SHELL SHAPE**

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It has repeatedly been observed that the morphology of ammonites follows a particular pattern of covariation. Within a given taxon, there will be gradation between compressed, involute, lightly ornamented forms and depressed, evolute, more heavily ornamented forms. This pattern is so well-established in widespread ammonite groups that Westermann dubbed it the First Buckman Law of Covariation. Several paleontologists have argued that there must be constructional constraints at work here—for example, the process of building a heavy rib might cause the shell to become more rounded.

On the other hand, while rib formation is generally assumed to be controlled by the genetic “growth program” of the individual, shell shape is often assumed to be susceptible to environmental influences, and controlled ecophenotypically. For instance, more compressed, streamlined individuals of a taxon are sometimes associated with higher current energy environments, while the rounder individuals are relegated to deeper, slower water.

This is Buckman's Paradox – are ornamentation and shell shape tightly linked, or is the morphogenesis of one factor controlled genetically, with the other factor controlled environmentally? If the First Buckman Law of Covariation holds, and holds specifically because the growth of a shell's form and ornamentation are tied together, we would expect that a taxon that shows a broad variation in shell shape should also show a broad variation in rib growth and form. Morphometric analyses of acanthoceratid ammonites from the Cenomanian-Turonian Western Interior Seaway of North America do not confirm this claim. Variability of rib characters and of the ontogenetic trajectories for rib width and spacing are not related to variability in shell shape characters. Hence, while some aspects of shell and rib growth may be related (and both constructionally and ecologically constrained), such a link is not reflected in the patterns of variability shown by these features.

These results suggest that controls on ornament and shell shape are different, at least in part. Buckman's covariation certainly exists, and has been well-documented in many ammonite groups. However, the exact nature of this covariation, and what causes it, is unclear. A sufficient and complete explanation for Buckman's covariation requires more, and more detailed, studies of ammonoid morphogenesis.

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